

THE ANATOMY OF THE SUBGENUS *BEDDOMEA* AND THE
RELATIONSHIPS OF THE GENUS *AMPHIDROMUS*.

By HENRY A. PILSBRY, Sc.D., etc.

Read 14th December, 1900.

PLATE XVI.

THE subgenus *Beddomea* was established by G. Nevill¹ for the reception of a few *Bulimi* from Ceylon and southern India, grouped around *B. Ceylanicus*, Pfr., as the type species. The relationships of the group have been variously estimated. Nevill himself says: "Very closely allied to *Amphidromus*, altogether distinct from *Geotrochus*; it takes the place of the former in southern India and Ceylon, where *Amphidromus* does not occur at all." Mr. Hugh Fulton, in his "List of the Species of *Amphidromus*," remarks that *Beddomea* and *Pseudopartula* appear "to be, from their conchological characters, sufficiently distinct to stand apart."²

The receipt of specimens preserved in formaldehyde, from Mr. O. Collett, enables me to present data showing the affinities of *Beddomea* to be with *Amphidromus*. Three species have been investigated: '*Bulimus*' *Ceylanicus*, Pfr., from Colombo; *B. intermedius*, Rve., from Watawala; and *B. albizonatus*, Rve., from Galle.

1. *AMPHIDROMUS (BEDDOMEA) INTERMEDIUS (Rve.)*.—The reproductive system (Pl. XVI, Fig. 2) opens in the usual position near the right tentacle. The atrium is small and short. The penis is slender below, enlarging distally, the terminal half very much and irregularly enlarged. Its internal walls, plicate below, become smooth near the apex of the lumen (Fig. 2*a*). The penis terminates in an epiphallus (*epi.*) scarcely shorter than the penis; near its base the retractor muscle is inserted. Penetrating the penis, the epiphallus ends in a very large and fleshy papilla, filling the penial cavity (Fig. 2*a*); beyond the epiphallus there extends a long flagellum (*fl.*), the major portion of which is coiled in a plane, there being about three spiral turns. The vas-deferens is convoluted at the beginning of its free portion. The vagina is long; spermatheca oblong, near the heart, on a long duct, which is slender above, swollen below. Other female organs are as usual.

The lung (Fig. 6) is rather elongate. The pulmonary vein is destitute of large branches, the venation is densest on the intestinal side and near the pneumostome as usual, but well developed upon the cardiac side of the lung also.

The kidney is very long and narrow, fully four times the length of the pericardium, and two thirds that of the lung, while the width

¹ Hand List Moll. Indian Museum, i (1878), p. 127.

² Ann. & Mag. Nat. Hist., ser. vi, vol. xvii (1896), p. 66.

of kidney and ureter together is one-tenth of the length. The reflexed ureter is as wide as the kidney. The rectal ureter seems to be a closed tube throughout.

The muscles are as described below for *A. albizonatus*. As in that species, the retractor of the right eye passes outside both branches of the genitalia.

The jaw is as described below for *A. Ceylanicus*, but has fewer ribs.

The radula (Pl. XVI, Fig. 4) is of the form usual in Helices; transverse rows of teeth meeting at a wide angle in the middle. The rhachidian and admedian teeth (Fig. 7, *R* to *3*) have single, long, broadly rounded cusps. These pass by transitions (Fig. 7, *15*) into the lateral type, in which the body of the tooth is inclined, and bears a three-lobed cusp (Fig. 7, *25*).

2. AMPHIDROMUS (BEDDOMEA) ALBIZONATUS (Rve.).—The genitalia in this species (Fig. 5) agree with those of *A. intermedius* in general features, but differ in the proportions of the parts. The penis is much smaller distally, containing a smaller papilla. The epiphallus is abruptly folded upon itself, the two portions being bound together. Both of these organs are about as long as in *A. intermedius*, and in both species the penis and epiphallus are about equal in length. The flagellum in *A. albizonatus* is much shorter, only two-thirds the length of the penis plus the epiphallus, while in *A. intermedius* it much exceeds their united length; it lies in longitudinal folds, not spirally coiled. The duct of the spermatheca is also shorter than in *A. intermedius*. The vagina seems to be shorter, though since this was broken in dissection, I do not venture to give its length.

The venation of the lung is similar to that in *A. intermedius*, except that the chief branches of the pulmonary vein stand out less obliquely. The borders of the veins are black-pigmented, as in *A. intermedius*.

The kidney is about four times the length of the pericardium, and over three-fourths that of the lung.

The retractor of the penis is attached to the diaphragm, as usual. The pharyngeal retractor is united to the right ocular and pedal band far forward; the left ocular and pedal and the tail retractor are free (Pl. XVI, Fig. 1). The right ocular retractor muscle passes outside (to the right of) the genitalia, not between its branches.

The jaw was lost. Teeth substantially as in *A. intermedius*.

3. AMPHIDROMUS (BEDDOMEA) CEYLANICUS (Pfr.).—The specimen examined was sexually immature, but the characteristic long flagellum and spermatheca-duct were observed, showing the species to be substantially similar to *A. intermedius* and *A. albizonatus* in its genitalia.

The lung is not pigmented, the venation is consequently faint. It is also sparser, and almost wanting on the cardiac side of the lung.

The kidney is shorter than in *A. intermedius*, a little less than four times the length of the pericardium, and about two-thirds that of the lung.

The jaw (Pl. XVI, Fig. 3) is well arched, thin, with its lower margin crenulated by the termination of thirteen, or fourteen flat 'ribs,' which seem separated by narrow intervals in the median part, contiguous or slightly overlapping towards the ends. It is just such a jaw as exhibited by some species of *Papuina* intermediate between the plaited and ribbed types.

DIMENSIONS OF THE PALLIAL ORGANS, IN MILLIMETRES.

	Length of lung		Length of pericardium		Length of kidney		Width of kidney and ureter
<i>A. intermedius</i> ...	37	...	6	...	25	...	2.5
<i>A. albizonatus</i> ...	27	...	5.5	...	22	...	3
<i>A. Ceylanicus</i> ...	28	...	4.8	...	18	...	2

DIMENSIONS OF THE GENITALIA.

	Length of penis		Length of epiphallus		Length of flagellum		Length of vagina		Length of spermatheca and duct
<i>A. intermedius</i> ...	11	...	10	...	27	...	7.5	...	32
<i>A. albizonatus</i> ¹ ...	10	...	11	...	14	...	—	...	22

From the foregoing it will be seen that the three species investigated agree in all important characters, while differing in various minor points. Compared with *Amphidromus* (*s.s.*), the subgenus *Beddomea* agrees in external characters, the long, band-like kidney, the pattern of lung reticulation, the arrangement of muscles (except as noticed below), the entire reproductive system, and the jaw. I have also been unable to find any differences between the central nervous system of *Amphidromus intermedius* and *Amphidromus* as figured by Wiegmann.

Beddomea differs from *Amphidromus* (1) in having the right ocular retractor passing to the right of both branches of the genitalia, not between them: (2) in having the cusps of the teeth on the median field of the radula broadly rounded and simple, instead of deeply cloven into ento-, meso-, and ecto-cones, as all the laterals are in *Amphidromus*; the marginal teeth of *Beddomea*, however, are cloven, and like those of *Amphidromus*; they also resemble the marginals in *Papuina*: (3) in having the radula longer in proportion to its breadth than it is in *Amphidromus*.

In view of the general agreement, it scarcely seems well-advised to accord *Beddomea* higher rank than that of a subgenus of *Amphidromus*. None of the three structural differences mentioned is of much importance, though I do not doubt that they will prove constant in *Beddomea*. When some of the species of *Amphidromus* which are conchologically nearest *Beddomea* (such as *A. sylheticus*) come to be examined, transitions may not unlikely be found in the dentition.

¹ The specimen of *A. albizonatus* was rather small, though mature; length of shell, 25 mm. A larger individual would, of course, give increased dimensions for the organs, without changing their proportions.

In the long flagellum, *Beddomea* is more like the larger, amphidrome species of *Amphidromus* than the smaller, invariably sinistral species, which, so far as known, have this organ much shorter.

The further affinities of *Beddomea* may then be considered in connection with those of *Amphidromus* proper.

Thanks to Semper, Jacobi, and Wiegmann, we have sufficient data to demonstrate beyond controversy the family relationships of *Amphidromus*, although up to the present time no adequate use has been made of them. Wiegmann has given a summary of the structure of the genus,¹ showing, although he does not make the comparison: (1) that it has the tripartite structure of male genitalia (penis, epiphallus, and flagellum) of the epiphallogonous Helices (such as *Camæna*, *Chloritis*, etc.), and also female organs of the same helicoid type: (2) that the external anatomy, nervous system, and retractor-muscle system are similar to those of the Helices: (3) that the kidney is long, narrow, and band-like, four to seven times the length of the pericardium: (4) that the jaw is between the aulacognath and weakly odontognath types, just as in the arboreal *Papuina* species.

In my "Guide to the Study of Helices,"² I have set forth the characteristics of the genitalia of epiphallogonous Helices, and need only mention here that *Amphidromus* agrees completely with my group *Epiphallozona* or *Camæninæ* in its reproductive organs. It agrees with no known group of 'Bulimi' or Bulimulidæ.

With regard to the pallial organs, some further statement is necessary. A large mass of data and drawings, still unpublished, shows that these organs supply facts for phylogenetic research not less in importance than those derived from the genitalia. While the *Helicinæ* (*Belogona*) have a short, tongue-shaped or sub-triangular kidney, the *Epiphallozona* (*Camæninæ*) have the kidney long and narrow, ribbon-like, exactly as in *Amphidromus*, and the general pattern of lung reticulation is also the same.³ All known 'Bulimi' and Bulimulidæ, including *Orthalicinæ*, have a short, triangular, or tongue-shaped kidney.

¹ "Landmollusken (Stylommatophoren): Zootomischer Teil": Abhandl. Senck. naturf. Ges., xxiv (1898), Heft 3, pp. 514-519. A splendid contribution to our knowledge of snail anatomy.

² Manual of Conchology, ser. II, vol. ix.

³ It may be worth while to give briefly some data supporting this statement. In *Planispira* the narrow kidney is at least two-thirds the length of the lung, and exceeds the pericardium from about four to six times in length (Wiegmann, *t.c.*, p. 489). In *Albersia (pubiceps)* the kidney is narrow, and more than four times the length of the pericardium (Wiegmann, *t.c.*). *Papuina vitrea* has a kidney about five times the length of the pericardium (Wiegmann, *t.c.*, p. 510). *Thersites Mitchellæ* has a long narrow kidney (length 36, width in the middle 5 mm.) four times the length of the pericardium, which measures 9 mm. long. In *Camæna (Camænella) platyodon* the kidney is also long and band-like, nearly four times the length of the pericardium, and two-thirds that of the lung. *Ganesella* has an extremely long and narrow kidney, varying in different species from five to ten times the length of the pericardium (Jacobi, "Jap. beschalte Pulmonaten": Journ. Coll. Sci. Japan, vol. xii, pt. 1). In *Pleurodonta (Caracolus) rostrata* the kidney is between five and six times the length of the pericardium, is very narrow, and tapers anteriorly.

The jaw and dentition of *Amphidromus* resemble those of certain forms of *Papuina*; though as I have shown in the "Guide to the Study of Helices," all arboreal Helices tend to form broad, gouge-like cusps to the teeth, either by enlargement of the middle cusp of each tooth or of all three cusps; and arboreal genera of demonstrably diverse ancestry sometimes converge towards a common type of dentition. For this reason, mere similarity of teeth is not necessarily a proof of genetic relationship.

Enough has been said to show that *Amphidromus* has no affinity to the Bulimulidæ or the 'Bulimi' of either hemisphere. It is unquestionably a member of that division of the Helicidæ which I characterized as the *Epiphallozona*, or *Camæninæ*; and it differs from such well-known genera as *Chloritis*, *Thersites*, and *Papuina* in very little besides the elongated shell. In conchological features, however, it is strongly differentiated and individualized.

EXPLANATION OF PLATE XVI.

- FIG. 1. Retractor muscles of *Amphidromus albizonatus*. *ph.r.* retractor of the pharynx; *p.r.* pedal retractors; *r.o.r.* right ocular retractor; *t.r.* tail retractor or columellar muscle (spirally coiled).
- „ 2. Genitalia of *A. intermedius*. *epi.* epiphallus; *fl.* flagellum.
- „ 2*a.* Distal end of penis of same, opened to show the papilla.
- „ 3. Jaw of *A. Ceylanicus*.
- „ 4. Outline of radula of *A. intermedius*, with a single row of teeth indicated.
- „ 5. Genitalia of *A. albizonatus*.
- „ 6. Pallial organs of *A. intermedius*. *k.* kidney; *u.* ureter.
- „ 7. Teeth of *A. intermedius*. Groups from the median, transition, and lateral portions of the radula.

NOTE.—Figures 1, 2, 5, and 6 are twice the natural size; the others magnified in various degrees.